

Population history in third millennium BC Europe: assessing the contribution of genetics

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Abstract

Several recent high-profile aDNA studies have claimed to have identified major migrations during the third millennium BC in Europe. This contribution offers a brief review of these studies, and especially their role in understanding the genetic make up of modern European populations. Although the technical sophistication of aDNA studies is beyond doubt, the underlying archaeological assumptions prove relatively naive and the findings at odd with more ‘traditional’ archaeological data. Although the existence of past migrations needs to be acknowledged and fully considered by archaeologists, it does not offer neither a robust explanatory factor, nor an enduring platform for interdisciplinary dialogue between archaeology and genetics. Alternative hypotheses are briefly explored.

Key-words

aDNA – Yamnaya - Corded Ware – Bell Beaker - demography

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Introduction

Since the 1960s, the rejection of migration as an explanatory mechanism for changes in the past has become one of the best examples of the theoretical versatility of archaeologists, prone to embrace new theories and repudiate former loved ones. And indeed, after several decades of denial, human mobility has crept its way back to the forefront of the archaeological agenda thanks to the development and application of several techniques, in particular strontium (Sr) and oxygen (O) isotope analysis (e.g. Bentley 2006). Unfortunately, after a brief period of fashion and fame, such studies have come under criticism because of rushed interpretations, whereby the apparent possibility of assigning clear geographical origins to individuals led to archaeological sensationalism, partly fueled by the implicit pressure of funding bodies and popular media, (Pollard 2011). Hopefully, the situation will get better, as archaeologists learn to act within the limits of the method and to reconsider the role of various forms of human mobility (see also Lightfoot and O'Connell 2016).

This paper argues that a similar story is potentially unfolding with genetics. Genetics, whether on modern or on ancient DNA (hereafter aDNA), offers new ways to identify past migrations and demographic events by relating genetic ancestry between different individuals, and ultimately the corresponding parent populations, across space and time. This field holds immense promise, as demonstrated by countless studies on plants (Brown et al. 2014), animals (Larson and Fuller 2014) and humans (e.g. Haber et al. 2016 and further references below). But when it comes to the latter, the situation becomes increasingly difficult and controversial, as genetics-led papers have raised more than a few eyebrows within the archaeological community. Hofmann, for instance, points out the mixed reception by *Linearbandkeramik* (LBK) specialists to aDNA; these genetic studies force archaeologists to reconsider the issue of migrations of early farmers (see below), but they are also compatible with more ‘interpretive’ issues such as identity (Hofmann 2015).

The focus here lies on Europe during the third millennium cal. BC, for which the narrative set forth in several high-profile publications seems at first sight to rise from the darkest depths of culture-history, full of migrations of eastern European pastoralists speaking Indo-European languages. This paper does not aim either to introduce the technical complexities of aDNA, nor to discuss all facets of the increasingly complicated emerging genetic pattern (see Haber et al. 2016). The objective is rather to highlight some key findings and associated assumptions found in this fast-moving literature and, beyond a mere critical appraisal of some of its shortcomings, to see how aDNA raises fundamental archaeological questions regarding population history. This paper is in many respects a call for archaeologists and geneticists to further embrace – and respect - each other's work.

An Early Neolithic detour

In order to understand the nature of aDNA research for the third millennium BC, a detour via the European Early Neolithic is necessary. The earliest use of DNA by archaeologists can be traced back to Ammerman and Cavalli-Sforza's work on the neolithisation of Europe (Ammerman and Cavalli-Sforza 1984). They showed a similarity between, on the one hand, the East-West diffusion of early farming as inferred from radiocarbon dates and, on the other hand, an East-West cline apparent in selected modern genetic traits. Ammerman and Cavalli-Sforza suggested that both patterns were causally linked as, in their opinion, the spread of the early farming corresponded to a demic process which they expected to have left a genetic signature of some sort.

This putative causal link was further elaborated upon during the 1990s by advocates of a ‘new synthesis’ bringing together archaeology, genetics and historical linguistics (e.g. Renfrew 1992). Renfrew first suggested that the spread of the Neolithic across Europe, and its assumed demic dimension, was responsible for the introduction of Indo-European languages (Renfrew 1987), a controversial claim whose repercussions are still being felt today (e.g. Bouckaert et al. 2012, Pereltvaig and Lewis 2015). A systematic link between demic diffusion, plant and animal

domestication, and the dispersal of linguistic families was then generalised and applied worldwide by Peter Bellwood (2005). Whilst these grand narratives were backed by apparent greater sophistication in all disciplines, many critical voices pointed out the naivety of several core assumptions (e.g. unquestioning use of ethnic groups as meaningful units of analysis: MacEachern 2000), and also the loose criteria used for correlating these diverse strands of evidence (e.g. Sims-Williams 1998). A key issue was the lack of chronological control over genetic evidence. Chronologies solely based on modern genetic data rely upon a so-called ‘molecular clock’, determined from estimate rates of mutations. This clock, while of use for geological time-periods (Busby et al. 2012), proves hard to calibrate and comes with significant uncertainty so that the contemporaneity between genetic and archaeological – let alone linguistic – processes cannot be independently demonstrated. Despite its ambition, and the academic weight and stubborn determination of its founders, the ‘new synthesis’ never really took off.

Although the existence of – either occasional or systematic – links between archaeological, genetic and linguistic data remains open to debate (see below), the problem of the chronological discrepancy between genetic and archaeological evidence has now been solved thanks to the development and widespread application of aDNA. In this case, the genetic signal is directly extracted from ancient samples of known date. Yet, modern genetics did not become obsolete overnight; quite the contrary because a key objective, for geneticists at least, remains the understanding of factors responsible for shaping modern genetic variation. Since the first successful attempts during the early 1980s (e.g. Pääbo 1985), aDNA as a field of inquiry has grown exponentially and now covers the entire spectrum of human prehistory (see review in Rizzi et al. 2012). Technical advances are continuously made, from the selection of suitable tissues (e.g. new preference for petrous bone; Pinhasi et al. 2015), to the extraction and sequencing of DNA (e.g. from mtDNA only to full genome: Haak et al. 2015), and statistical treatment of the vast quantities of information thus created (e.g. Patterson et al. 2012). All in all, aDNA studies make for a fast-moving and, to untrained archaeological eyes, intimidating literature.

Unsurprisingly, the Early European Neolithic became a laboratory to test the archaeological relevance of aDNA. Early on, mtDNA results for LBK samples from Germany, Austria and Hungary demonstrated that the LBK was associated with genes unknown in either Palaeolithic or Mesolithic Europe (Haak et al. 2005). Further work on LBK (Haak et al. 2010), Starčevo-Körös-Criș (Szécsényi-Nagi et al. 2015) and Anatolian Neolithic sites (Mathieson et al. 2015) have confirmed this initial result and proved without doubt a certain element of reality in the claims made by Bellwood, Renfrew, Ammerman, Cavalli-Sforza, and Childe to name but a few: the introduction of early farming in Europe cannot be disentangled from the migration of farmers whose origins are to be sought in the Near East. In many cases, the genetic signature is such that we are entitled to talk

about large-scale migration, although the exact size and nature of change is still open to discussion and is likely to differ from one region to the next. For all their crucial contributions to the field, it must be stressed that aDNA results do not settle all controversies regarding the European Early Neolithic, but rather steer research into new directions (Hofmann 2015).

These aDNA studies have also led to the – less expected – conclusion of a lack of genetic continuity between the LBK and modern-day European populations, suggesting that ‘demographic processes after the early Neolithic have contributed substantially to shaping Europe's contemporary genetic make up’ (Haak et al. 2010, 7). In a way, more migration than many (processual and post-processual) archaeologists would be willing to contemplate must have happened during European Later Prehistory. Several recent studies have sought to identify these later prehistoric demographic events, for instance through changes in mtDNA diversity (see below). But major results have only recently been achieved through the sequencing of full ancient genomes, thus widening the scope of genetic variation.

While various levels of admixture between Mesolithic and early Neolithic groups – and between Neolithic groups (e.g. Rivollat et al. 2015) – can be identified, the genetic variety of modern European populations cannot be accounted for solely in those terms. In particular, modern admixture suggests a contribution, at one point in the past, of a population genetically related to Native Americans (Patterson et al. 2012). On the basis of full genomic analysis of Mesolithic and early Neolithic individuals, Lazaridis and others (2014; but see Fu et al. 2016) demonstrated that modern European human genetic variation could be satisfactorily explained by the admixture of three ancient, highly differentiated meta-populations, labelled as Ancient North Eurasian (ANE, represented by a sample from the Upper Palaeolithic site of Mal'ta, Russia), Western European Hunter-Gatherer (WHG, represented by a sample from the Late Mesolithic site of Loschbour, Luxemburg), and Eastern European Farmer (EEF, represented by a sample from the Early Neolithic/LBK site of Stuttgart). Whilst the WHG and EEF genetic components match those of the western European Mesolithic and central European Early Neolithic in date and origin, the question, from a genetic point of view, lies in when and where the ANE component was introduced into the European genome.

Genes and third millennium BC

While earlier aDNA papers cover the fifth and fourth millennium BC (e.g. Lacan et al. 2011, Lee et al. 2014), the drive to identify this hypothetical third genetic component largely explains the recent focus on the third millennium BC. Figure 1 shows the distribution of 230 Eurasian samples for which full genomic information is available (Mathieson et al. 2015). Although it represents a selection of existing aDNA data, this map offers an accurate representation of the current patchy state of knowledge (compare with Brandt et al. 2015: figure 1). Sampled sites are clustered in

northern and central Europe, as well as western Russia. There is a lack of sampled sites in the Mediterranean, with a few exceptions in northern Spain and northern Italy. This situation is largely explained by the poor preservation of aDNA in dry climates, a problem that may be overcome by systematic sampling of the petrous bone (Pinhasi et al. 2015).

Before detailing the role of the third millennium BC in the modern genetic make up, it is worth noting that such long-term perspective is not the only scale at which aDNA can contribute to our knowledge of the past. Studies on the third millennium BC have produced insights at the site-specific rather than continent-wide scale, drawn from analyses of the genetic diversity of the corresponding funerary populations. At Eulau (Saxony-Anhalt), archaeological excavations revealed four late Corded Ware multiple burials, all containing varying combinations of adults, males and/or females, and children (Meyer et al. 2009). These unusual deposition practices, in a funerary world otherwise dominated by single graves, and the fact that several individuals exhibited signs of lethal interpersonal violence suggest that these people were the victims of a violent raid, and were carefully buried by the survivors. This interpretation is reinforced by aDNA which demonstrates biological relationships between individuals placed in the same grave, including one nuclear family comprising one man, one woman and their two children (Haak et al. 2008). Although the exceptional character of the site cautions against generalising this result across the entire Corded Ware Complex, it suggests a partial homology between biological, social and funerary groupings (Meyer et al. 2009). Interestingly, a contrasting picture emerges from the contemporaneous nearby Bell Beaker site of Kromsdorf (Lee et al. 2012). Located c. 50km from Eulau, Kromsdorf is classified as Bell Beaker based upon ceramic typology and funerary practices (i.e. bodies placed on a North-South axis). aDNA from six individuals shows that these all belong to distinct mtDNA haplogroups, suggesting 'that burial practices at this site did not place importance on maintaining shared maternal relations in a mortuary context' (Lee et al. 2012: 577).

Although based upon two examples, the differences between the aDNA results from Eulau and Kromsdorf bring new elements to the complex relationship between Corded Ware and Bell Beaker complexes in central Europe (Vander Linden 2006). Given the objective of this paper, it is however more important to highlight that such results, focusing on intra-site rather than regional analysis, are probably less controversial and easier to accept for archaeologists as they echo long-standing interests in identity and social dimension of funerary practices.

When considering the impact of the third millennium BC on modern European genetic make up, Central Germany plays a leading role. The Mittelbe-Saale region has been the focus of targeted aDNA sampling, allowing the creation of a unique time-transect across the local Neolithic (c. 5400 – 2300 cal. BC) and Early Bronze Age (c. 2300 – 1800 cal. BC) sequence, comprising 364 individuals for 25 sites (Early Neolithic: 154 individuals, 10 sites; Middle Neolithic: 78 individuals,

9 sites; Corded Ware: 57 individuals, 7 sites; Bell Beaker: 31 individuals, 7 sites; EBA; 113 individuals, 12 sites; Brandt et al. 2013). It must be noted that these data cover mtDNA and, sometimes, Y-chromosome, but not entire genomes. Analysis of this dataset lead to the identification of four key events shaping mtDNA diversity (Brandt et al. 2013). Event A corresponds to the LBK culture and the appearance of mtDNA haplogroups of eventual Near-Eastern origin, whilst Event B (broken down to B1 and B2, dated to c. 4100 and c. 3100 cal. BC) is related to the neolithisation of the Northern European plain and associated with an increased presence of mtDNA haplogroups found amongst local Mesolithic groups. Events C and D relate respectively to the Corded Ware Complex and the Bell Beaker Phenomenon. Event C is marked by the introduction of two mtDNA haplogroups (I, and U2), absent from the Early and Middle Neolithic. Although the overall sample size is limited, the probability of the occurrence of these haplogroups as a by-product of sampling bias is statistically ruled out. Other documented haplogroups are already present in the local Mesolithic and Neolithic, but with changing frequencies (e.g. T1). These elements, as well as the presence of Y-chromosome haplogroup R1a1a, point to similarities with South Siberia and Kazakhstan, and suggest East-West movement (Brandt et al. 2013). By contrast, Event D is characterised by the disappearance of haplogroups I and U2 in favour of a high proportion of haplogroup H. This haplogroup is the most frequent mtDNA haplogroup in Europe today, and was also prevalent in Iberia since the Mesolithic, suggesting a potential gene flow from South-West Europe to central Europe (see also Brotherton et al. 2013; see below). The Early Bronze Age picture is intriguing, with the renewed presence of haplogroups of I, U2 and T1, possibly inherited directly from the Corded Ware. Brandt and others suggest that this situation could result from admixture between Corded Ware and Bell Beaker groups, and sex-biased migration of Bell Beaker males into central Europe (Brandt et al. 2015). The genetic evidence for this last claim is the identification in Kromsdorf of Y-haplogroup R1b, which, according to Brandt and colleagues ‘has a proposed origin and current geographic distribution very similar to mtDNA haplogroup H’ (Brandt et al. 2015: 86; quoting Myres et al. 2011). Although published recently, these publications have, in the fast-changing world of aDNA, been supplanted by papers based upon full genomic sequencing (Allentoft et al. 2015; Haak et al. 2015; Mathieson et al. 2015; Cassidy et al. 2016). Whilst previous contributions generally focus upon mtDNA, partial or full genome sequencing marks a noticeable shift in aDNA research, allowing much finer analysis.

Sequencing of samples from Russia demonstrates that local hunter-gatherers (pre 5500 BC) cluster together (so-called EHG group) and are genetically close to the suggested parent ANE population (Haak et al. 2015). This EHG component is present at a later date in individuals belonging to Yamnaya culture, who show a complex genetic history with traces of admixture with a population related to the Near-East (Haak et al. 2015), as well as ancestry linked to Late Upper Palaeolithic and

Mesolithic Caucasian hunter-gatherers (Jones et al. 2015). Interestingly, and especially so given the complexity of its make up, a genetic signal comparable to this ‘Yamnaya ancestry’ is absent during the Early and Middle Neolithic in central Germany, but is well-represented amongst 25 Late Neolithic (both Corded Ware and Bell Beaker) and Bronze Age individuals from the same region. The sudden appearance of this ‘Yamnaya ancestry’ demonstrates the westwards movement of people, the scale and structure of which can be assessed by other facets of the genetic evidence. Firstly, as this new component is not found in older local Neolithic cultures, either drift or continuous gene flow can be ruled out. Secondly, the high proportion of Y haplogroup R1b in both Russian data (100%) and LN/BA central European data (60%) suggests East-West diffusion and, together with other statistical tests, that both sexes contributed to this genetic signal (Haak et al. 2015). Yet, there was not a complete population replacement, but rather a mixture between the Yamnaya and local populations, so that this ‘Yamnaya ancestry’ contributes to up to 79% of the Corded Ware sample (Haak et al. 2015). The complexity of this pattern is reinforced by the fact that, when compared to the Corded Ware signal, both Bell Beaker and Early Bronze Age samples demonstrate a lower frequency of this ‘Yamnaya ancestry’, together with a resurgence of genetic components present during the Early and Middle Neolithic.

The case for an influx of people originating from Russia in central Europe is compelling, especially as the same signal has been independently identified by another team, using slightly different methods and different samples. Allentoft and others report traces of this ‘Yamnaya ancestry’ in Bell Beaker samples from Germany and Czech Republic, as well as Early Bronze Age samples from Sweden, Hungary and Poland, and Late Bronze Age Montenegro (Allentoft et al. 2015). Likewise, the same genetic component has been identified in three individuals buried at the beginning of the second millennium BC on Rathlin Island, Northern Ireland (Cassidy et al. 2016). However, evidence of this ‘Yamnaya ancestry’ is not ubiquitous and is lacking amongst samples from the Iberian sites of El Mirador (fourteen individuals dated to c. 3000-2600 BC: Gómez-Sánchez et al. 2014, Mathieson et al. 2015) and El Portalón (six individuals dated to c. 3200-2600 BC, one individual dated to c. 2200-2000 cal. BC, one individual dated to c. 1700-1500 cal. BC: Günther et al. 2015). This absence suggests that either the ‘Yamnaya ancestry’ was introduced in the Iberian Peninsula in the late third millennium BC or after (Mathieson et al. 2015), or that Chalcolithic and/or Bronze Age Iberian population diversity was higher than expected (see also Gómez-Sánchez et al. 2014). It is worth pointing out that the site of El Mirador, though contemporaneous with the earliest Bell Beaker expressions (Cardoso 2014), did not yield any material culture related to this archaeological complex.

It goes without saying that the genetic and population history of Europe did not come to an end with

the Late Neolithic and Early Bronze Age. However, all publications agree that this period was instrumental in setting the genetic diversity ancestral to the modern European situation (e.g. Ricaut et al. 2012). Later changes surely occurred, but would not have had similar wide-ranging effects – ‘the presence of all major mtDNA haplogroups by the end of the Neolithic makes it increasingly difficult to discern recent demographic changes and would require larger population events to have an observable effect and/or full mitochondrial genome sequencing to detect more subtle changes’ (Brandt et al. 2013, 261; see also Allentoft et al. 2015, 170).

Genetics, linguistics...

While the congruent identification of this ‘Yamnaya ancestry’ in numerous locations across Late Neolithic and Bronze Age Eurasia by distinct aDNA research groups is an extraordinary discovery which requires the full attention of archaeologists, another more disturbing aspect links together these studies as the researchers seek to identify the spread of Indo-European languages. This bold conjecture is made explicit in one of the titles (‘Massive migration from the steppe was a source for Indo-European languages in Europe’ : Haak et al. 2015), whilst Allentoft and others discuss it in a distinct section (Allentoft et al. 2015: 170), and Cassidy and others only – but still – in a single sentence of their penultimate paragraph (Cassidy et al. 2016). The issue is extensively discussed by Brandt and others (Brandt et al. 2015) who, incidentally, are all listed as co-authors on the Haak et al. 2015 paper.

As already stated, integrating archaeology, genetics and linguistics is as difficult as it is ambitious a task, and previous attempts have all been met with extensive criticisms. Fully aware of this strained relationship, Brandt and others state that, as far as genetics is concerned, the ‘props of the edifice are not as shaky’ as they were fifteen years ago, and that advances in aDNA provide ‘a solid genetic framework against which archaeological and linguistic models can be tested’ (Brandt et al. 2015, 87). In a cautious way, they point out that the identification of two major migration events at the beginning and at the end of the Neolithic are compatible with both main archaeological competing hypotheses about the spread of the Indo-European languages: on the one hand, Colin Renfrew's Anatolian hypothesis equating the diffusion of farming with Indo-European languages (Renfrew 1987) and, on the other hand, the Steppe hypothesis defending major population movements from the North-Pontic steppes during the fourth and third millennium BC, a position mostly associated with the late Marija Gimbutas (1977), James Mallory (1989) and David Anthony (2007). By contrast, Haak and others (2015) unilaterally back the Steppe hypothesis by stressing that Renfrew's initial proposal rests upon the suggested lack of migrations after the Early Neolithic (but see Renfrew 1999). In this sense, the existence of a population flow from the east to central Europe during the third millennium BC would not only refute one of Renfrew's key arguments, but also ‘make a compelling case for the steppe as a source of at least some of the Indo-European languages

in Europe' (Haak et al. 2015, 210; see also Allentoft et al. 2015).

The increased technical sophistication of aDNA might well be undeniable, yet the rest of the methodological apparatus has not evolved in any significant way. And although archaeological cultures, genetic components and linguistic families seem to mirror each other superficially, this similarity does not hold with deeper consideration of their respective natures (see also Pereltsvig and Lewis 2015). While cautionary statements can be found in some of these palaeogenomics studies against the generalisation of the archaeology – genetics – linguistics equivalence (Allentoft et al. 2015, 171; Brandt et al. 2015, 88), their emphasis on the Indo-European problem contradicts this prudence. At first impression, it is difficult to escape the feeling that the game is rigged in the sense that, since the realms of each discipline are so large, a correlation can be found if you look for one. The mistake here lies in the mirage of a grand synthesis, aiming 'at a fallacious congruity of material culture, language and genes' (Bandelt et al. 2003, 105), rather than the exploration of the partial overlap between each discipline and their specific realms of inquiry (Vander Linden 2015). Rather than generalising the results from one – admittedly technically proficient – discipline to others, as is effectively happening now, one is left to wonder whether or not these findings should not be treated on equal footings and combined with data and interpretations from other disciplines, such as linguistics or archaeology.

...and archaeology?

Leaving aside linguistics and Indo-European languages for the time being (see Anthony and Ringe 2015), the main question raised by recent aDNA papers for archaeologists is as old as it is simple: to what extent do migrations provide an explanation for past processes documented by archaeology? And, as a consequence, do migrations offer a robust platform for an enduring dialogue between geneticists and archaeologists?

Most archaeologists would probably consider that these aDNA studies are inherently biased towards migrations because of their over-reliance upon 'archaeological cultures'. The intimate relationship between migration and 'archaeological culture' may well feature in any archaeological handbook, but it is worth remembering that the concept of 'archaeological culture' was initially developed as a classificatory tool by antiquarians facing increasing amount of data, a process that happened within a pre-existing culture-historical intellectual framework (Vander Linden and Roberts 2011). The term might thus be heavily laden with migrationist views, but it does not necessarily lead to them. In practice, many archaeologists merely consider archaeological cultures as a convenient short-hand term for which there is no consensual alternative. From this point of view, archaeological cultures are not *de facto* homogeneous wholes, but labels pointing towards material patterns worth studying (see contributions in Roberts and Vander Linden 2011).

This last dimension seems to be, if not ignored, at least glossed over in most aDNA papers. It must

be noted that some of the statistical techniques used in aDNA research, such as Principal Component Analysis (PCA), do not rely upon pre-existing cultural labels tagged to individual samples (as explicitly pointed out by Fu et al. 2016). The recognition of potential patterns lies in the location of samples on the PCA chart, which, in an ideal way, should echo temporal and/or geographical proximity. Obviously, the wider relevance of such results is ultimately dependent upon the range of sampling which, at least now, often remains relatively limited. It is at this stage that the noted over-reliance upon archaeological cultures comes into play, as patterns identified from geographically restricted sampling are then generalised across the entire area of the corresponding archaeological culture. The use of archaeological cultures as classificatory units thus enables a shift from – generally – local to regional or supra-regional scale. Yet, by doing so, one has to assume implicitly a relative homogeneity of the archaeological culture which, especially in the case of the 3rd mill cal. BC is particularly damaging as at least two of the archaeological cultures under scrutiny here, Corded Ware and Bell Beaker, are first and foremost characterised by their variability.

The Corded Ware complex occupies a vast territory stretching across northern and central Europe, and is dated to c. 2900-2000 cal. BC. Archaeological descriptions of this complex have long stressed its uniformity and linked it to putative migratory movements (e.g. Kristiansen 1989). Such uniformitarian accounts largely rest upon the identification of the so-called A-horizon, a set of typologically identical grave goods found across the entire distribution area, and generally interpreted as the earliest phase of the complex and the material trace of a migration (e.g. Buchvaldek 1986). Yet, absolute dating and typological re-examination of the regional sequences demonstrate that each component of the A-horizon was developed independently in distinct areas and came to be widely shared at a later stage (Furholt 2003, 2014). The rest of the material record follows the same pattern: each material trait presents a different distribution, and constitutes part of a network of widely shared and integrated items and practices (Furholt 2014). A broadly similar conclusion can be reached for the Bell Beaker Phenomenon, dated between c. 2800 and 2200 cal BC, and distributed across western and central Europe. Older archaeological explanations have often privileged a single or limited range of material traits upon the wider available record (Vander Linden 2013), and explanations in terms of migrations have long been favoured, Iberia being a preferred candidate for a ‘Bell Beaker homeland’ (Jeunesse 2014). Yet, over the past two decades or so, numerous studies have rather insisted upon the variability of all aspects of the archaeological record, from ceramic technology and morphology (e.g. Besse 2003, Všíanky et al. 2014), to arrowheads (Bailly 2014) (see also Vander Linden 2006).

For both Corded Ware Complex and Bell Beaker Phenomenon, the emerging archaeological picture is thus one dominated by variability and wide-ranging networks, the structure of which remains largely to be explored. It is noteworthy that this conclusion applies to the entire distribution of both

archaeological cultures, and is thus at odds with the implicit assumption made by archaeogenetics that results gained at a local scale can be generalised across larger regions, so that mass migrations become a logical and necessary explanation. It is in this confusion of scales that the main tension between archaeology and genetics lies. Although archaeologists have been wrong in denying any role for human mobility in European prehistory, it remains however obvious that mass migration does not suffice to account for the entire complexity documented by archaeology. While we can reasonably expect that further aDNA sampling will improve the geographical and temporal resolution and lead to more subtle patterns, the issue of conflicting scales needs to be tackled head-on and multiple explanatory factors must be considered by geneticists and archaeologists alike.

Fitness, marriage, demography

This last section explores three alternative hypotheses to explain the variability encountered in the archaeological record as well as the various levels of genetic admixture amongst third millennium BC European populations. In many respects, these all share the same starting point, by seeking how changes in genetic make-up translate in terms of population history, not simply understood in terms of amplitude and geographical origins of individuals undertaking long-term relocation, but critically in terms of the conditions of possibility and causal factors that would have structured human mobility. Whilst the first two hypotheses are not very satisfactory, but necessary for the sake of the overall argument, the third one offers a wider range of possibilities.

Hypothesis one assumes that the success of these new genetic components is not related to the mass arrival of new people, but rather, after introduction by few newcomers, to an evolutionary advantage, either to be sought in the genes themselves or in the associated material traits. Obviously, there is no denying that genes, or artefacts for that matter, can move independently without large scale movement of people. But, in tune with the extensive archaeological variability, the question is whether or not a first, limited, movement of individuals followed by large-scale dissemination amongst local populations could explain the identified genetic patterns. Full genome sequencing indeed allows the in-depth assessment of phenotypes, and to evaluate selective pressure on certain traits (Mathieson et al. 2015). Although for instance a selection for height can be observed among steppe populations (Mathieson et al. 2015), nothing in the genetic 'Yamnaya ancestry' explains its diffusion in terms of evolutionary fitness. Likewise, neither the Corded Ware Complex nor the Bell Beaker Phenomenon are clearly associated with a given technology or economic change that would explain their widespread distribution (Vander Linden 2006, 167; Furholt 2014, 81).

Hypothesis two relates the diffusion of genes to sex-biased transmission (e.g. restricted marital rules). This possibility has been ruled out on genetic grounds for the Corded Ware Complex (see above;), but suggested for central German Bell Beakers (Brandt et al. 2015). Their key argument

lies in the identification in Kromsdorf of Y-chromosome haplotype R1b, for which an Iberian origin was suggested, a region where numerous archaeologists also place the 'Bell Beaker homeland' (Jeunesse 2014). Genome-wide sequencing now invalidates this hypothesis as the geographical origins of R1b haplogroup seem to lie in the steppe area (Haak et al. 2015). The lack of unambiguous genetic signal associated with sex-biased transmission actually echoes the absence of gender patterning in human mobility demonstrated by Sr studies across the entire Bell Beaker distribution area (e.g. Price et al. 2004, Evans et al. 2006, Boel 2011; see also for the Corded Ware Sjögren et al. 2016 who report possible female exogamy, although the sex ratio of local / non-local individuals does not present any statistical significance). The period is indeed characterised by high frequency of human mobility, in some exceptional cases over long distance (Fitzpatrick 2011) but which concerns in equal measure men and women, ruling out the presence of consistent post-marital relocation rules.

Hypothesis three assesses the role of regional demographic regimes in shaping genetic diversity. Demography has been overlooked for the third millennium BC, but recent evidence, including summed calibrated date probability distributions, points to the complexity of the period from this point of view. The validity of summed calibrated date probability distributions as population proxy is debated (e.g. Bamforth and Grund 2012, Williams 2012, Contreras and Meadows 2014), but several papers suggest that this method is reliable when coupled with extensive numerical simulations and other proxies (e.g. Whitehouse et al. 2014, Woodbridge et al. 2014, Vander Linden et al. submitted for publication). The studies quoted here are thus only taken as possible indications of local population fluctuations, using the technique as an exploratory tool as initially intended (Rick 1987). For the Corded Ware Complex, data from northern Europe point to a very contrasted regional picture, with some areas possibly experiencing a rise in population, some a marked drop (Hinz et al. 2012, figure 3), a situation echoed by changes in settlement and land use patterns (Lechterbeck et al. 2014). Lillios and colleagues report for South-Western Iberia a peak in summed radiocarbon dates between 3000 and 2500 cal BC followed by a sharp drop, while South-Eastern Iberia experiences a continuous growth throughout the third millennium BC (Lillios et al. 2015, figure 5). For the Bell Beaker period, population increase is suggested in Britain by summed calibrated date probability distributions and a contemporary episode of woodland clearance (Woodbridge et al. 2014), and a comparable signal seems to occur in Ireland (Whitehouse et al. 2014: fig. 20; see also McLaughlin et al. 2016). The record is admittedly very patchy, but, together with the high frequency of human mobility, it seems that third millennium BC Europe is characterised by diverse local demographic regimes, possibly paralleled by extensive reshuffling of individuals. In this hypothesis, regional differences in population density would provide the basis for human mobility, including migrations, between and across small and large geographic spaces,

accompanied by changes in cultural and social structures.

While hypotheses one and two cannot explain as such the current state of archaeological and genetic affairs, hypothesis three provides more possibilities. It must be stressed that this hypothesis is not exclusive to migrations; quite the contrary, in this hypothesis the patterns observed in recent aDNA studies are indeed largely accounted for by long-term relocation of individuals. But the key differences rather lie in the scale, range and direction of this mobility. If a westwards gene flow from the North Pontic steppes seems likely for the introduction in central and western Europe of the aforementioned third genetic component, other contrasted mobility events, as suggested by the levels of admixture observed for the Bell Beaker period and the Early Bronze Age, probably occurred. This scenario should not be considered as relying upon even more migration than current interpretations by archaeogeneticists. It rather asks for a re-appraisal of multiple forms of mobility and population trajectories, whereby regional differences play a structuring role in the ebb and flow, not only of genes and people, but also of practices and ideas.

Conclusion

aDNA is an innovative and impressive field which has profoundly altered our understanding of the past. As one of its results, archaeologists cannot deny anymore the existence of migrations during Later European Prehistory. This being said, migrations, and especially mass migrations, still do not explain in any satisfying way the structure of the large-scale archaeological complexes which flourish during the third millennium BC. How are we to account for this disjuncture between archaeologists' doubts and the apparent certainties of geneticists? Either material culture and genes – and languages for that matter – behave in such alien ways that the interdisciplinary dialogue has to be restricted to those rare cases where all signals match each other; or, as argued here, alternative hypotheses have to be sought by all disciplines. More attention should in particular be paid to the various geographical scales, by shifting the focus from one-size-fits-all explanations to the identification of multiple mechanisms at play, under local variants, across larger areas. Such mechanisms would aim at explaining the profound archaeological divergences between central and western Europe, and, from the genetic point of view, the various levels of admixture. From this point of view, the demographic regimes under which genetic and material changes occurred are worth re-exploring in detail (see Shennan 2012).

Such research would need archaeologists to go back to the drawing board, and geneticists not only to fill in the existing geographical gaps in sampling, but also to consider a wider range of archaeological questions. The focus on migrations might have been a successful strategy in terms of high-ranking publications and media coverage, but, as admitted by geneticists themselves, it is at best a short-term option. Of all social sciences, archaeology has probably the most elaborated interdisciplinary ethos, built into many facets of its everyday practice, which could provide a robust

basis for a continuing, constructive dialogue with archaeogeneticists

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Figure caption

Figure 1: Distribution of 230 genome-wide samples from Eurasia. Black dots: Mesolithic – white squares: Neolithic – white triangles: Chalcolithic / Bronze Age (after Mathieson et al. 2015, supplementary materials; samples from central Asia are omitted)

Short biography

Dr Marc Vander Linden is a specialist of European Later Prehistory. After graduating from the Université Libre de Bruxelles, he has held post-doctoral positions in Cambridge, Leicester and currently London. His interests cover variability of the archaeological record, the – still relevant – use of archaeological cultures, and demography. After initially focusing on the Late Neolithic, and especially the Bell Beaker Phenomenon, he now works mostly on the early Neolithic, with corresponding field activities in Bosnia and Herzegovina and Montenegro.